

SONGS OF SONG SPARROWS: REACTIONS OF MALES TO SONGS OF DIFFERENT LOCALITIES

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Song in birds is generally associated with territorial defense, reproduction, and maintenance of the pair bond (Thorpe 1961; Marler and Hamilton 1966). Since the songs of most species are distinctive even to the human ear, it has long been supposed that they aid in the reproductive isolation of one species from another (Marler 1960). The males of many species have been found to react to playback of a song of their own species in a manner typically including vocalizations, movement toward the sound source, and visual displays. Other species' songs do not elicit such reactions (Dilger 1956; Thielcke 1962; Lanyon 1963; Stein 1963; Gill and Lanyon 1964; Ficken and Ficken 1967; Lemon and Herzog 1969; Thompson 1969; Schubert 1971; Emlen 1972).

As well as the differences between species, dialects or consistent differences between nearby populations may occur within the songs of one species. Dialects have been shown to exist in a wide variety of songbirds, including the Chaffinch (*Fringilla coelebs*) (Marler 1952), Short-toed Tree Creeper (*Certhia brachydactyla*) (Thielcke 1961), Great Tit (*Parus major*) (Compertz 1961), White-crowned Sparrow (*Zonotrichia leucophrys*) (Marler and Tamura 1962), Mistle Thrush (*Turdus viscivorus*) (Isaac and Marler 1963), Cardinal (*Cardinalis cardinalis*) (Lemon 1966), Pyrrhuloxia (*Pyrrhuloxia sinuata*) (Lemon and Herzog 1969), Chingolo (*Zonotrichia capensis*) (Nottebohm 1969), Indian Hill Mynah (*Gracula religiosa*) (Bertram 1970), Rufous-sided Towhee (*Pipilo erythrophthalmus*) (Kroodsma 1971), and Vesper Sparrow (*Pooecetes gramineus*) (Kroodsma 1972). Behavioral responses to dialects have not been widely studied, but in the species which have been investigated, responses were stronger to songs of the birds' own dialects, as in the Cardinal (Lemon 1967), the Indian Hill Mynah (Bertram 1970), and the White-crowned Sparrow (Milligan and Verner 1971).

Each male Song Sparrow (*Melospiza melodia*) possesses a repertoire of several different

song patterns, each of which is repeated several times before another is begun. Although neighboring birds rarely have entire song patterns which are identical to one another, they usually have some elements within the patterns in common. Shared elements have been noted for birds in southern Quebec (Harris and Lemon 1972) and in Maine (Borror 1965), although Mulligan (1966) makes no such claims for birds in California. On the basis of these findings it appears that Song Sparrows have dialects in the same sense as other species, although the large amount of individual variation in the overall song patterns masks the similarities of neighbors' songs from the human listener.

This report compares the reactions of male Song Sparrows from three localities in southern Quebec to playback of songs recorded from their own locality versus songs recorded from a different locality. If dialects actually exist, then we should expect greater responses to the local songs than to those from a foreign location, as was found in the species previously studied.

METHODS

Recordings of male Song Sparrows were made at 7½ ips (19 cm per sec), using a Uher 4000 tape recorder with a Uher 516 microphone mounted in a 30-inch (76 cm) parabolic reflector. For playback, songs were transferred to endless tape loops recorded at 3¾ ips (9.5 cm per sec). These loops were played on a Uher 4000 tape recorder, which was used with a Fanon-Masco 12-w amplifier and an Atlas HU-12N horn with a 100-ft (30-m) cable. The loudspeaker was placed near the center of each bird's territory, with an observer standing approximately 30 ft (9 m) away.

Responses of territorial males to playback were observed at three locations in southern Quebec (fig. 1): Parc Cote Ste. Catherine, Knowlton, and Caughnawaga. Parc Cote Ste. Catherine provided a varied and optimal habitat on a long, narrow strip of land between the St. Lawrence River and the South Shore Canal. Ponds and marshes were interspersed with shrubs, grassy meadows, and forested areas. The density of male song sparrows in the location at which playback took place was 3.5 birds per acre (8.5 per ha). The nearby location at Caughnawaga,

5 miles (8 km) W of Parc Cote Ste. Catherine, provided a similar habitat, though without the open water, in an abandoned lot. It supported a density of 2.4 males per acre (5.9 per ha). The Knowlton location, 55 miles (89 km) E of Parc Cote Ste. Catherine, was more marginal. The Song Sparrows were restricted to low-lying areas bordering farmland; the density of birds there was 1.2 per acre (3.1 per ha).

Each individual was exposed to three conditions on successive days, presented in random order: (1) a control period in which no recordings were played; (2) a recording of a local song; and (3) a recording of a foreign song. Each test began only after the birds had remained silent for at least 1 min. Behavior was then noted for a total of 6 min in each case. For the sessions with playback of the local or foreign song, a recorded song was repeated at 10-sec intervals during the first 3 min. For the control sessions without song, the procedure followed was the same as in the sessions with song playback; the tape recorder, loudspeaker, and observer were positioned in the same places and 1 min of silence was imposed prior to the 6-min observation period.

Since banding Song Sparrows usually involves attracting them to mist nets by playing recorded songs, it was decided not to risk altering their responses to playback by disturbing them with such a procedure. Identification of individual males was therefore made on the basis of location of singing. Although some misidentification may have occurred, such cases were probably rare. Both Nice (1937) and Tompa (1964) found male Song Sparrows to be faithful to their territories: Nice recorded a case of desertion by a breeding male only once, and Tompa in only 7 out of 160 males over a period of three breeding seasons.

CATEGORIES OF RESPONSE TO PLAYBACK OF RECORDED SONGS

When songs of their own species were played within their territories, male Song Sparrows generally reacted by singing, by flying near the loudspeaker, and by giving call notes and displays. The categories of response measured in the playback experiments included: number of songs in the first 3 min of observation (during playback in the sessions with song playback); number of songs in the second 3 min (immediately after playback in the sessions with song); latency of singing during the first 3 min to the nearest 5 sec; latency of approach to within 15 ft (5 m) of the speaker during the first 3 min; closest approach during the first 3 min; and closest approach during the second 3 min. Distances greater than 15 ft were given a rank of 0; within 15 ft but greater than 6 ft (2 m), a rank of 1; within 6 ft but greater than 3 ft (1 m), a rank of 2; and within 3 ft, a rank of 3. The above categories of response were chosen because of their relative ease of observation and quantification. Other types of response, such as displays and number of changes in orientation toward the loudspeaker, were excluded because the birds' movements were often obscured from view. Frequency of calling was not counted because the call notes often occurred at rates too rapid to count easily.

Nonparametric statistics (Siegel 1956) were used in comparing responses to different song types since they make no assumptions about the shapes of the sampling distributions or about homogeneity of variance.

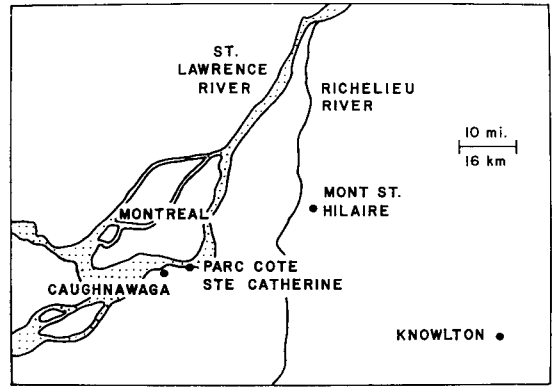


FIGURE 1. Map showing areas of study.

RESULTS

EXPERIMENT 1: PLAYBACK AT PARC COTE STE. CATHERINE

The responses of 21 male Song Sparrows at Parc Cote Ste. Catherine to songs of nearby and distant locations were compared over a period of 5 days (12–16 May 1971) early in

TABLE 1. Responses of male Song Sparrows in Experiment 1 at Parc Cote Ste. Catherine to playback of songs of local and foreign dialects.^a

Response category	Local song			Foreign song		
	Subgroup			Subgroup		
	1	2	3	1	2	3
Songs during playback	7	1	0	1	0	0
	7	1	12	1	0	8
	4	1	0	10	0	0
	0	12	1	1	13	1
	21	3	2	15	2	2
		13	15		0	1
		15	0		10	23
		2	15		20	0
(Kruskal-Wallis)	H = 0.73			H = 0.80		
(two-tailed)	0.50 < P < 0.70			0.50 < P < 0.70		
Songs after playback	10.0	8.9	11.0	5.8	4.8	4.8
	H = 0.12			H = 0.15		
	0.90 < P < 0.95			0.90 < P < 0.95		
Latency of song, sec	81.0	32.5	80.6	59.0	110.0	115.6
	H = 1.29			H = 2.84		
	0.50 < P < 0.70			0.20 < P < 0.30		
Latency of approach, sec	80.0	49.4	53.1	81.0	88.1	118.8
	H = 0.25			H = 0.58		
	0.80 < P < 0.90			0.70 < P < 0.80		
Approach rank during playback	1.8	2.8	2.6	1.8	1.8	1.4
	H = 2.53			H = 0.52		
	0.20 < P < 0.30			0.70 < P < 0.80		
Approach rank after playback	1.6	2.3	1.4	1.2	1.4	0.8
	H = 2.27			H = 1.13		
	0.30 < P < 0.50			0.50 < P < 0.70		

^a Each subgroup was exposed to playback of a different pair of song patterns (fig. 2). Values for individual birds are shown for the first category, and thereafter only means for each subgroup are given.

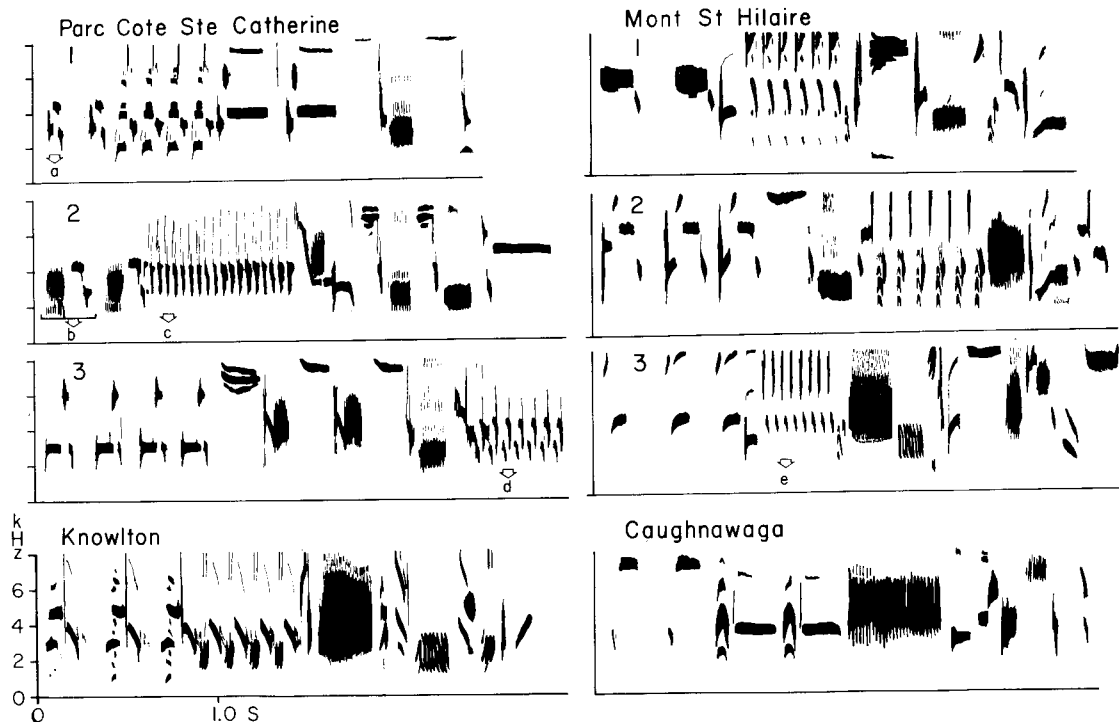


FIGURE 2. Wide-band sonograms of the songs used for playback. Those from Parc Cote Ste. Catherine were used as local songs, and those from Mont. St. Hilaire as foreign songs, in playback to subgroups 1, 2, and 3 in Experiment 1 (at Parc Cote Ste. Catherine). That from Knowlton was the local song for Experiment 2 (at Knowlton) and the foreign song for Experiment 3 (at Caughnawaga). That from Caughnawaga was the foreign song for Experiment 2 and the local song for Experiment 3. Small letters indicate syllables discussed in text.

the breeding season, that is, after pair formation but before nesting. Territories by then were well established, and by limiting the testing period to a few days, possible variations in response related to the progression of the nesting cycle were minimized. For use in playback, local songs were recorded from birds inhabiting a location within Parc Cote Ste. Catherine which was approximately 0.5 miles (0.8 km) from the study area. Foreign songs were recorded at Mont. St. Hilaire, 23 miles (37 km) E of Parc Cote Ste. Catherine (fig. 1).

Within the group of 21 birds were three subgroups, each of which heard different song patterns to represent the local and the Mont. St. Hilaire dialects (fig. 2). The purpose of this procedure was to determine whether different song patterns within a particular locality exerted different effects. As table 1 shows, there was considerable individual variation in response; for example, the number of songs given per individual in subgroup 1 ranged from 0 to 21 during playback of the local song pattern, and from 1 to 15 during playback of the foreign song. Similar ranges occurred in the other categories. Taken as a

whole, however, the responses of the subgroups were similar, as shown by the Kruskal-Wallis one-way analysis of variance. Because there proved to be no significant differences among the subgroups in any of the six categories of response when either local or foreign song patterns were considered, for subsequent analysis the three subgroups were combined.

On the combined data, the Friedman two-way analysis of variance revealed significant differences among the conditions of control, foreign songs, and local songs in all categories of response (table 2). This significance resulted largely from much higher response levels during playback of both types of songs than during control sessions. The number of approaches was most strongly affected by playback: when no song was played, only one bird approached within 15 ft of the speaker during the first 3 min; this individual flew to a nearby tree 30 sec after the test period started and remained there for approximately 4 min while singing a total of 18 songs. In contrast, 14 birds approached during playback of the Mont. St. Hilaire songs and 19 during playback of the local songs. An examination of the mean ranks of approach in

PARC COTE STE
CATHERINE n = 21

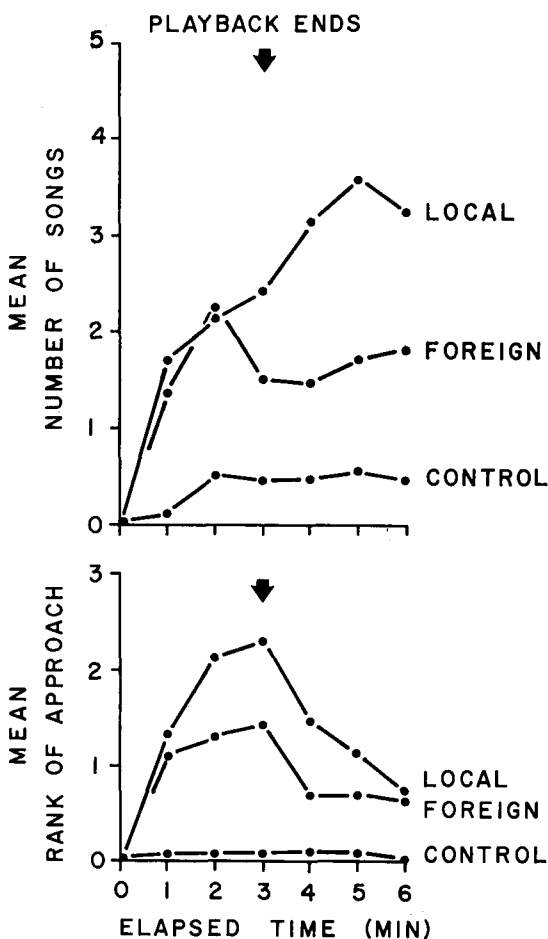


FIGURE 3. Experiment 1, Parc Cote Ste. Catherine: mean number of songs (above) and mean ranks of approach (below) in each minute of observation for local dialect, foreign dialect, and control conditions.

each minute (fig. 3) showed that they remained near zero at all times in the control, whereas the ranks increased during playback and dropped afterwards.

In all but one category, the birds responded significantly more to playback of a local song than to a song from Mont. St. Hilaire, as was shown by the Wilcoxon test (table 2). Only the number of songs during playback did not differ significantly between the two areas. A more detailed analysis of the number of songs for each 1-min interval during and after playback (fig. 3) revealed that for the first 2 min the mean number of songs increased at about the same rate for both areas, but thereafter only the local songs evoked further increase. Also, each minute showed that approach ranks both during and after playback

TABLE 2. Reactions of 21 male Song Sparrows in Experiment 1 at Parc Cote Ste. Catherine to conditions of no playback (control), playback of a foreign song, and playback of a local song.

Response category	Condition		
	Control	Foreign song	Local song
Songs during playback or first 3 min of control	\bar{x} 1.1 χ_r^{2a} 7.3 T ^b 50.5(41)	5.1 $P < 0.01 < P < 0.025^c$ $P > 0.05$	6.3
Songs after playback or second 3 min of control	\bar{x} 1.5 χ_r^{2a} 12.6 T 29.5(41)	5.0 $P < 0.005$ $0.01 < P < 0.025$	10.0
Latency of song, sec	\bar{x} 151.4 χ_r^{2a} 11.6 T 43(47)	100.0 $P < 0.005$ $0.025 < P < 0.05$	62.4
Latency of approach, sec	\bar{x} 172.9 χ_r^{2a} 20.9 T 58.5(68)	98.1 $P < 0.005$ $0.01 < P < 0.025$	58.1
Approach rank during playback or first 3 min of control	\bar{x} 0.1 χ_r^{2a} 21.6 T 39(41)	1.6 $P < 0.005$ $0.025 < P < 0.05$	2.5
Approach rank after playback or second 3 min of control	\bar{x} 0.1 χ_r^{2a} 16.2 T 16.5(26)	1.1 $P < 0.005$ $0.01 < P < 0.025$	1.8

^a χ_r^{2a} : Friedman two-way analysis of variance of the three conditions.

^b T: Wilcoxon matched-pairs signed-ranks test of foreign versus local songs (critical values at $P = 0.05$ indicated in parentheses).

^c One-tailed levels of probability are given.

were higher to the local song than to the foreign one.

Thus the birds at Parc Cote Ste. Catherine clearly responded to playback of both local and foreign songs and exhibited higher response levels to the local songs. The lessened responses to foreign songs may have reflected either a drop in responsiveness by all individuals or an absence of response in a few individuals, while those which did respond continued to do so at levels comparable to the local songs. Five birds neither sang nor approached during playback of the foreign song, whereas only two showed a similar lack of response during playback of the local song. When these birds were discounted and Wilcoxon tests were performed on the remaining 14 individuals, responsiveness was still found to be higher to the local songs, the differences being significant in three categories (number of songs after playback, latency of song, and rank of approach after playback) and close to significance in the others. Thus it appears that the response to foreign songs reflects a

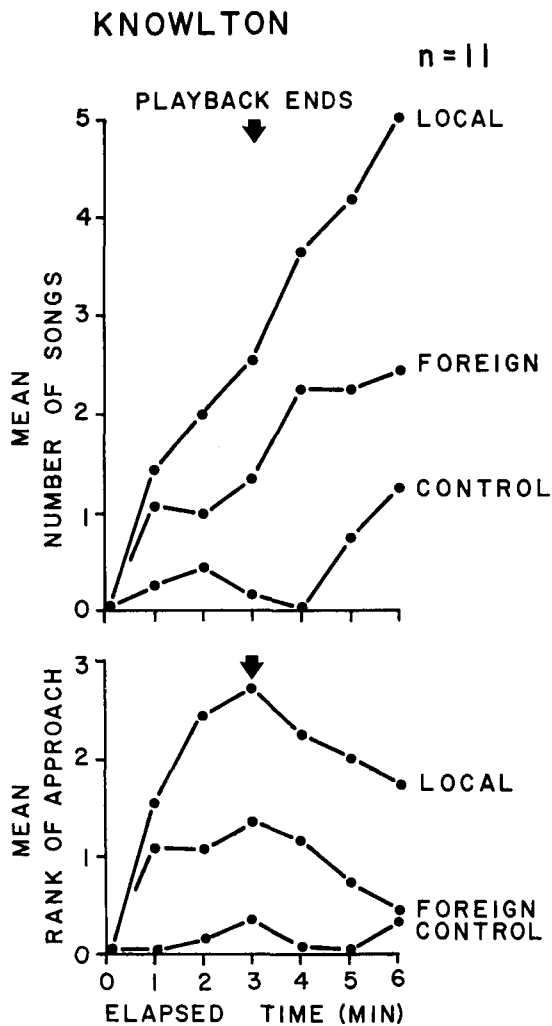


FIGURE 4. Experiment 2, Knowlton: mean number of songs (above) and mean rank of approach (below) in each minute of observation for local dialect, foreign dialect, and control conditions.

general decreased responsiveness throughout the population which includes an increased likelihood that responses will be absent altogether in certain individuals.

EXPERIMENT 2: PLAYBACK AT KNOWLTON

The discrimination of songs shown by the males at Parc Cote Ste. Catherine was not determined solely by peculiarities of that population. In a later experiment performed from 22 to 26 May 1972, 11 birds at Knowlton responded less to a song from Caughnawaga than to a local song (fig. 2). The latter was recorded from a bird within the Knowlton population whose territory was not immediately adjacent to any of the birds tested. The nesting status of the birds was uncertain at this time.

In this experiment, responses to playback

TABLE 3. Reactions of 11 male Song Sparrows in Experiment 2 at Knowlton to conditions of no playback (control), playback of a foreign song, and playback of a local song.

Response category	Condition		
	Control	Foreign song	Local song
Songs during playback or first 3 min of control	\bar{x} 0.9 χ_r^2 4.7 T 3.5(4)	3.5 $0.025 < P < 0.05$ $0.025 < P < 0.05$	6.0
Songs after playback or second 3 min of control	\bar{x} 2.0 χ_r^2 4.2 T 12(8)	7.0 $0.05 < P < 0.10$ $P > 0.05$	12.8
Latency of song, sec	\bar{x} 165.0 χ_r^2 4.2 T 12.5(6)	90.0 $0.05 < P < 0.10$ $P > 0.05$	97.3
Latency of approach, sec	\bar{x} 165.0 χ_r^2 7.1 T 10(14)	116.4 $0.01 < P < 0.025$ $0.01 < P < 0.025$	48.2
Approach rank during playback or first 3 min of control	\bar{x} 0.5 χ_r^2 11.8 T 0(4)	1.4 $P < 0.005$ $P = 0.01$	2.8
Approach rank after playback or second 3 min of control	\bar{x} 0.5 χ_r^2 9.1 T 5.5(8)	1.2 $0.005 < P < 0.01$ $0.01 < P < 0.025$	2.4

of either of the two songs were again much greater than to no playback (table 3). A Friedman two-way analysis of variance showed significant differences among the three conditions in four of the six categories of response: number of songs during playback, latency of approach, and approach ranks during and after playback. The same four categories showed significantly greater responsiveness to the local song in the Wilcoxon test. The mean number of songs during the second 3 min was greatest to the local song, but differences were not significant. Mean latency of song was slightly less to the foreign song, but not significantly so.

A minute-by-minute analysis of mean number of songs (fig. 4) showed that in contrast to the Parc Cote Ste. Catherine birds, where singing decreased once playback of the foreign song stopped, the means for the Knowlton birds increased throughout the 6-min observation period for both local and foreign songs. The means were consistently greater for the local than the foreign song, both remaining at higher levels than the control. The graph of mean ranks of approach in each minute

TABLE 4. Reactions of 14 male Song Sparrows in Experiment 3 at Caughnawaga to conditions of no playback (control), playback of a foreign song, and playback of a local song.

Response category	Condition		
	Control	Foreign song	Local song
Songs during playback or first 3 min of control	\bar{x} 0.7 χ_r^2 2.9 T 30.5(14)	3.3 $0.10 < P < 0.15$ $P > 0.05$	3.1
Songs after playback or second 3 min of control	\bar{x} 3.5 χ_r^2 4.8 T 26.5(17)	6.5 $0.025 < P < 0.05$ $P > 0.05$	7.8
Latency of song, sec	\bar{x} 153.2 χ_r^2 2.2 T 27.5(14)	100.4 $0.15 < P < 0.25$ $P > 0.05$	112.9
Latency of approach, sec	\bar{x} 180.0 χ_r^2 15.4 T 45(21)	76.1 $P < 0.005$ $P > 0.05$	74.6
Approach rank during playback or first 3 min of control	\bar{x} 0.0 χ_r^2 16.7 T 5(4)	1.5 $P < 0.005$ $P > 0.05$	2.1
Approach rank after playback or second 3 min of control	\bar{x} 0.0 χ_r^2 14.7 T 0(8)	0.7 $P < 0.005$ $P < 0.005$	1.7

showed a form similar to that of the Parc Cote Ste. Catherine population: with both recorded songs the ranks increased steadily throughout the 3-min playback and dropped off afterward, while remaining consistently highest to the local song.

EXPERIMENT 3: PLAYBACK AT CAUGHNAWAGA

The same song patterns played at Knowlton (fig. 2) were played to 14 males at Caughnawaga; the bird from which the local song had been recorded again was not an immediate neighbor to any of the birds tested. Nesting had begun by the time this experiment took place, which was from 29 May to 5 June 1972.

As in the previous experiments, responses were generally much greater during the two playback situations than during the control, and a Friedman test showed differences between the three conditions to be significant in four of six categories, exceptions being the number of songs during the first 3 min and the latency of song (table 4). The Wilcoxon test, however, revealed few differences between the two playback conditions. Only in

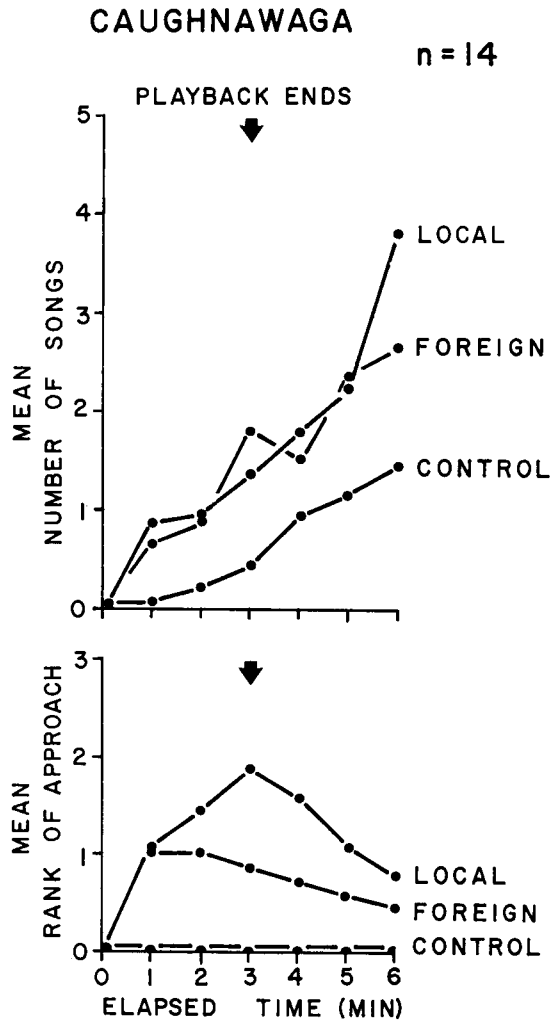


FIGURE 5. Experiment 3, Caughnawaga: mean number of songs (above) and mean rank of approach (below) in each minute of observation for local dialect, foreign dialect, and control conditions.

approach ranks was responsiveness notably greater to the local song, and only after playback was it significantly greater.

The amount of singing in each minute, while greater to songs from both localities than to no song, showed no obvious differences between them except in the final minute (fig. 5). Mean ranks of approach in each minute, on the other hand, showed a similar differentiation between local song, foreign song, and control conditions to that shown by the Knowlton and Parc Cote Ste. Catherine populations.

CORRELATION OF MEASURES OF RESPONSE

So far the categories of response have been treated separately; however, calculation of Spearman coefficients of rank correlation for playback of local songs in the three experi-

ments indicated that in fact some categories were interrelated (table 5). Most strongly related of the response categories were number of songs during playback and latency of song, these being significantly correlated in all three experiments. As might be expected, the correlation was a negative one, large amounts of song being joined with short latencies of response. Ranks of approach during and after playback were significantly positively correlated at Caughnawaga and Knowlton and had a coefficient close to significance at Parc Cote Ste. Catherine. Also correlated in two locations, this time at Parc Cote Ste. Catherine and Knowlton, were the number of songs after playback with both the number of songs during playback and latency of song. At Parc Cote Ste. Catherine, latency of approach correlated significantly with latency of song and with number of songs during playback. At Caughnawaga, latency of approach was negatively correlated with ranks of approach during and after playback. No significant correlation was found in any of the experiments between approach rank during playback and latency of song or number of songs during playback.

The calculation of the correlation coefficients was interrelated in most cases, with the result that some statistically significant correlations are not very meaningful. For instance, at Parc Cote Ste. Catherine and Knowlton, when the number of songs after playback was correlated with the number of songs during playback and the number of songs during playback with latency of song, it is not surprising that the number of songs after playback was also correlated with latency of song. It is for this reason that certain correlations were omitted from table 5: (1) the number of songs after playback with approach rank during playback; (2) the number of songs after playback with latency of approach; (3) the approach rank after playback with number of songs during playback; and (4) the approach rank after playback with latency of song.

As the coefficients could not vary independently, one might expect their values to be similar relative to one another in the three localities. In order to ascertain the degree of similarity, a Kendall coefficient of concordance was calculated for the Spearman coefficients, which were ranked according to absolute value, disregarding the sign. Using this method, a Kendall coefficient of concordance (W) of 0.50 was obtained, giving a X^2 of 14.87 and P (two-tailed) $< 0.20 > 0.10$ (critical

TABLE 5. Spearman rank correlation coefficients between certain categories of response in Experiments 1, 2, and 3 when birds were exposed to local songs (P values two-tailed for $P \leq 0.05$).

Comparisons	Experiment 1 Parc Cote Ste. Catherine 1971 n = 21	Experiment 2 Knowlton 1972 n = 11	Experiment 3 Caughnawaga 1972 n = 14
No. songs during	+0.723	+0.823	+0.155
No. songs after	$P = 0.001$	$P = 0.002$	
No. songs during	-0.753	-0.888	-0.948
Latency of song	$P = 0.001$	$P = 0.001$	$P = 0.001$
No. songs during	-0.439	-0.197	+0.017
Latency of approach	$P = 0.046$		
No. songs during	+0.198	+0.359	+0.267
Approach rank during			
No. songs after	-0.749	-0.637	-0.255
Latency of song	$P = 0.001$	$P = 0.035$	
No. songs after	+0.128	+0.339	+0.352
Approach rank after			
Latency of song	+0.595	+0.298	+0.158
Latency of approach	$P = 0.004$		
Latency of song	-0.192	-0.359	-0.386
Approach rank during			
Latency of approach	-0.264	-0.352	-0.667
Approach rank during			$P = 0.009$
Latency of approach	-0.156	-0.236	-0.533
Approach rank after			$P = 0.050$
Approach rank during	+0.404	+0.638	+0.687
Approach rank after		$P = 0.035$	$P = 0.007$

value of X^2 at $P = 0.10$ being 15.99). Thus there appears to be a trend, though not a significant one, for response categories to be correlated in a similar manner in all three experiments.

TABLE 6. Responses of 21 male Song Sparrows tested at Parc Cote Ste. Catherine in Experiment 1 to the first and second playback of a recorded song, without regard to song pattern.

Type of response		First playback	Second playback
Songs during playback	\bar{x}	5.6	5.9
	T (Wilcoxon)		65 (41)
	P (one-tailed)		> 0.05
Songs after playback	\bar{x}	7.9	7.1
	T		67.5 (41)
	P		> 0.05
Latency of song, sec	\bar{x}	64.3	98.1
	T		50.5 (47)
	P		> 0.05
Latency of approach, sec	\bar{x}	71.4	84.8
	T		97 (68)
	P		> 0.05
Approach rank during playback	\bar{x}	2.2	1.9
	T		60 (41)
	P		> 0.05
Approach rank after playback	\bar{x}	1.5	1.4
	T		47 (26)
	P		> 0.05

LEVELS OF RESPONSE ON SUCCESSIVE EXPOSURES

One factor which might contribute to variability in responses to playback is the number of prior exposures to playback. To determine whether responsiveness changed in successive exposures, behavior to the first-played song of Experiment 1 was compared with that to the second-played, without regard to song type. In this experiment, intervals between the exposures ranged from 1 to 3 days. Although no statistically significant differences were noted in any categories, the mean number of songs given after playback was greater, latencies of singing and approach were less, and approach ranks during and after playback were greater, all on the first exposure, irrespective of the pattern played (table 6). The measure of latency of song came closest to significance with a Wilcoxon T value of 50.5 (critical value = 47). It appears then that repeated playback creates a slight lessening of responsiveness in Song Sparrows.

FREQUENCIES OF SYLLABLE TYPES IN EXPERIMENT 1

Since Song Sparrows can discriminate between local and foreign songs, there must exist some peculiarities within the songs designating the areas from which they come. Ideally, to discover what the peculiarities might be for the populations studied here, the model songs would have been compared with those sung

by each of the experimental birds. In practice, this would have been difficult to do because of the amount of time needed to obtain the complete song repertoires of all the birds. Nevertheless, the repertoires of 16 birds had been intensively studied in 1969 and 1970 at two locations within Parc Cote Ste. Catherine (Harris and Lemon 1972). Since playback in Experiment 1 took place at a nearby location only a year later, it is unlikely that the song characteristics in that area would have changed to any great extent. Therefore the frequencies of occurrence of syllable types (a syllable is here defined as a serially repeated unit within a song pattern) in the songs used for playback could be compared with their occurrence in these previously studied populations. The local song (Parc Cote Ste. Catherine) played to subgroup 1 contained three syllables, of which the introductory one (a, fig. 2) occurred in the repertoires of 6 out of the 16 Parc Cote Ste. Catherine birds previously studied; the two syllables of the foreign (Mont. St. Hilaire) song, on the other hand, occurred in none of these birds' repertoires. The local song played to subgroup 2 contained two syllables, the introductory one (b) occurring in 7 of the 16 birds and the second (c) in 12 of 16; the foreign song again contained no syllables occurring in these birds' repertoires. In subgroup 3, the local song contained three syllables, the third (d) occurring in 10 of the 16 birds; the foreign song contained two syllables, the second (e) occurring in one of the birds' repertoires. Therefore, all the local songs contained one or more syllables of frequent occurrence in the repertoires of Parc Cote Ste. Catherine birds, whereas the foreign songs contained syllables which were absent or rare.

DISCUSSION

Playback of their own species' song within the territories of male Song Sparrows affected behavior in all categories of response measured. When compared with conditions under which no song was played, the rate of singing by the territory-holders increased during and immediately after playback, their distance from the loudspeaker was less, and latencies of singing and approach were lower. A notable feature was the strong aftereffect of playback on rate of singing, which continued to increase to even higher levels after rather than during playback. The birds also showed a tendency to remain in the vicinity of the loudspeaker after playback, although this tendency declined rather rapidly. Residual effects of song

playback have also been noted for the Cardinal (Lemon 1967), White-throated Sparrow (*Zonotrichia albicollis*) (Falls 1969), White-crowned Sparrow (Milligan and Verner 1971), and Indigo Bunting (*Passerina cyanea*) (Emlen 1972).

The high correlation of the number of songs during playback with the latency of song in all three locations and with the number of songs after playback in two localities indicates that once song is begun there is a tendency for it to continue for some time; and indeed, under natural conditions, one often observes periods of frequent song alternating with periods of silence. For Song Sparrows, the intervals between bouts of different song patterns are normally greater than the intervals between songs of a given pattern (Mulligan 1966:23). The significant correlation of rank of approach during playback with rank after playback in two localities would indicate that these birds were not inclined to change their position relative to the stimulus even for some time after the stimulation had ceased. The general lack of correlation of measures of singing with measures of approach points out that these two response modes can vary independently of one another, and that high levels in one mode do not necessarily lead to high levels in the other. At Parc Cote Ste. Catherine and Knowlton the birds responded differentially between local and foreign songs in both singing and approach (figs. 3 and 4). At Caughnawaga, although the levels of approach showed a similar distinction, there was no differentiation in levels of singing (fig. 5).

Some habituation to the second playback occurred but was only pronounced in latency of song, which became longer on the second exposure. For this reason that category is probably not as desirable a measure of behavior as others when the experimental design requires more than one playback to each individual. Habituation to playback has also been observed in Great Tits (Gompertz 1968), White-crowned Sparrows (Verner and Milligan 1971), and Indigo Buntings (Emlen 1972); in the White-crowned Sparrows the phenomenon affects a wide range of behaviors including songs, flights, and approach time.

The great range in individual response levels precludes accurate prediction of a single bird's behavior on hearing playback and emphasizes the need for adequate sampling of the population. The variability in response is probably related to many factors, such as location of the loudspeaker within the territory, nesting and pairing status of the bird, age and condition

of the bird, activities of the bird prior to playback, and individual idiosyncracies.

Male Song Sparrows in these experiments were less responsive to foreign than to local songs: rates of singing were less; distances from the loudspeaker greater; and latencies of singing and approach longer. The differences were of degree rather than of kind since most birds responded to some extent to both types of songs in all categories. We attributed the lessened responsiveness to differences in the song characteristics of the sample populations and not just to individual differences in singing. Because the experimental subjects were separated from the birds providing the local songs for playback by at least one neighboring territory in Experiments 2 and 3, and by 0.5 mile in Experiment 1, the subjects were not likely to have had extensive experience with either of the songs used for playback. For this reason, and because variations in song patterns have been found to occur among populations of eastern Song Sparrows (Borror 1965; Harris and Lemon 1972), the differences in response are attributed to differences of dialect.

Other studies have also found a decrease in responses to foreign dialects: male White-crowned Sparrows sang less; made fewer flights; took longer to approach; and came nearer the speaker than when played the local dialect (Milligan and Verner 1971). Mynahs responded by less frequent flight, fewer calls, longer latency before the first response, and more playback calls ignored to call types characteristic of a different locality than to call types common in their own locality (Bertram 1970). In Great Tits, which have been shown by Gompertz (1961) to possess song dialects, populations from southern Germany reacted no more strongly in levels of approach and singing to songs from Afghanistan than to songs of another species (Thielecke 1969b). Cardinals in Ontario showed greater discrimination as the distance between dialect forms increased: none approached during playback of a Texas song pattern; a few approached on hearing a pattern from a nearby location in Ontario; and nearly all approached on hearing the local pattern (Lemon 1967). The degree of responsiveness to foreign dialects is probably affected by the amount of similarity in the two dialect forms presented, which in turn may be affected by such factors as distance between localities and rate of change in song structure over distance, the degree to which dialect changes affect whatever parameters of song are most impor-

tant in signalling the species, and the degree to which experience is important in the recognition of the species' song. That the responses to songs need not be all or none but can be graded is consistent with the concept of heterogeneous summation.

In contrast to the above studies which have found responsiveness to be greater to songs from localities nearer the subject of playback, other studies, performed on species not known to have dialects, have shown responsiveness to be greater to the songs of a stranger than to those of an immediate neighbor (Weeden and Falls 1959; Falls 1969; Emlen 1971). Response differences in this second type of study are probably caused by habituation to songs of the immediate neighbor. Similar work has not been performed to date on species showing dialect variation, although Bertram (1970) has found that Mynahs respond differently to songs of their mates than to songs of another bird of the same sex.

An interesting difference between the responses found for Song Sparrows in the present study and those found for White-crowned Sparrows by Milligan and Verner (1971) was in nearest approach to the loudspeaker; the White-crowned Sparrows came closer during songs of the foreign dialect, while Song Sparrows approached more closely during the local dialect. Milligan and Verner postulated that the local song may have induced a stronger tendency to flee in their birds than a foreign song. That this is obviously not the case with Song Sparrows may somehow be related to the greater degree of individual variation in their songs; whereas in White-crowned Sparrows most individuals of a population sing similar patterns, in Song Sparrows individuals rarely have entire patterns in common, and similarities within a population are only found in subunits of the songs.

At Caughnawaga, the differentiation between dialects was not as great as in the other two locations; of all the categories, only approaches were significantly different. Levels of singing for the foreign song were close to those in the other two locations, but levels for the local song remained low until the final minute of observation. The lesser differentiation shown by this population may have been related to the nesting status of the birds since the experiment was performed later in the season than at the other locations, or it may reflect peculiarities in the songs chosen for playback.

Differentiation in responses to different dialects may not be a universal phenomenon

in Song Sparrows. In late June 1970, six birds were tested at Mont. St. Hilaire with songs from the local population and from Lac Ste. Marie, 130 miles (209 km) W; levels of singing were high to both types of song and there were no differences in measures of approach. Although the sample size was not large and this experiment was performed relatively late in the breeding season, it does point to the possibility that not all Song Sparrow populations respond similarly to foreign dialects.

The present series of experiments did not tell us what parameters of the songs form the basis for dialect discrimination by Song Sparrows, but a previous study showed that particular syllables within the songs are frequently shared among neighboring birds and seldom between birds from more distant populations (Harris and Lemon 1972). In the local songs used for playback in Experiment 1, all contained at least one syllable type which occurred frequently at Parc Cote Ste. Catherine, whereas in the three foreign songs used, only one contained a syllable found at this locality, and it rarely occurred. If syllable structure is one of the parameters by which these birds distinguish dialects, then songs containing syllable types frequently heard by an individual may cause high levels of response, while songs containing few or no syllable types within the birds' experience may produce low levels.

Learning of singing patterns is known to be influential in the development of song in the young of several species showing dialects, for example, in Chaffinches (Thorpe 1961), Cardinals (Lemon and Scott 1966; Dittus and Lemon 1969), White-crowned Sparrows (Marler and Tamura 1962), and Song Sparrows (Mulligan 1966). Identification of the species through song is also known to depend to a great extent upon learning in some estrildid finches (Immelmann 1969). Learning of singing patterns and responsiveness to songs appear to be linked, at least in the Chaffinch. Hinde (1958) found that captive Chaffinches were stimulated to sing the most by songs like the ones which the bird itself had learned, and Stevenson (1969) found that Chaffinch song was a more effective reinforcer to birds which had previously been exposed to it than to birds which had been isolated. If the same is true for all birds showing dialects, then it is not surprising that field experiments have shown songs of the more familiar local dialect to be more stimulating than those of a foreign dialect with unfamiliar characteristics.

In attempting to apply the experimental results presented here to situations which might occur in nature, it must be considered that each bird heard playback of a given song for only one short period of time in his territory, and also that no rival male was present during the playback. Thus the visual stimuli normally associated with a singing bird were lacking and behavioral interactions were impossible. In a natural situation, with repeated exposure to songs associated with the visual and other auditory stimuli of a conspecific male, Song Sparrows may eventually come to react as strongly to songs from an entirely foreign repertoire as to songs of the local dialect. Nevertheless, these experiments do indicate that, at least in the initial exposure, the songs of an immigrant from a different dialect area are more likely to go unheeded by the local males than are those from their own area.

The function or functions of dialects may be related to reducing variability of the signal within a population and increasing the likelihood of recognition among neighbors (Lemon 1967; Thielcke 1969a), enhancing the integration of reproductive behavior in the pair and in the population (Nottebohm 1969), or restricting the movement of individuals and thus the size of the gene pool, making adaptation to specific habitats more efficient (Marler and Tamura 1962; Nottebohm 1969). The occurrence of dialects must be related to fidelity to a locality, but the causal relationship between the two events remains unclear. Nottebohm and Selander (1972) have suggested that Chingolos in Argentina are not panmictic and have proposed that dialects are an important factor in maintaining this situation. However, in other cases dialects may have developed simply because of the isolation of populations, which perhaps results from sedentariness of individuals or from geographic barriers to movement. In Song Sparrows, it is known that movement of individuals is low (Nice 1937, ch. 8; Johnston 1956; Tompa 1964), but until the appropriate studies of population dispersal patterns in relation to dialect patterns are performed on this and other species, it will not be evident how they affect and are affected by one another.

A clear understanding of the functional importance of dialects is also hampered at the present time by the relative lack of information on how they influence females' behavior. Milligan and Verner (1971) found more trills given by female White-crowned Sparrows to songs of their local dialect, and Bertram (1970) found that both members of pairs of

Mynahs responded more strongly to familiar call types. Such evidence supports the argument that the likelihood of pairing is greater if both male and female are familiar with the same dialect pattern. A captive female Great Tit from Afghanistan bred only reluctantly with a male of a different race (Gompertz 1968); however, since there were morphological as well as vocal differences in this case, it is hard to say what part was played by dialects in causing the breeding difficulties. For most species, the females' responses to song playback in general, and to dialects in particular, have not been studied.

SUMMARY

Male Song Sparrows at Parc Cote Ste. Catherine, Knowlton, and Caughnawaga, Quebec, showed discrimination between songs of local and foreign dialects in levels of response to playback. While most birds responded positively to playback of both songs, amounts of singing were greater, approach was nearer, and latencies of response were less to the local dialect. There was a notably strong residual effect of playback upon levels of singing. Some categories of response were highly correlated, particularly number of songs during playback with latency of song and with number of songs after playback and rank of approach during, with rank after playback. Some habituation to playback was evident in the second session. The discrimination of dialects could have been based on the syllable structures within the song patterns, since the songs used as the local dialect playback at Parc Cote Ste. Catherine contained syllables frequently heard in birds' repertoires there whereas the songs used as the foreign dialect did not.

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